

Putting a crinoid on a stalk: new evidence on the Devonian diplobathrid camerate *Monstrocrinus*

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Non-technical Summary.—*Monstrocrinus* is a most unusual crinoid from the Devonian of Germany. It has long, simple to complex spines attached to most calyx plates. A stem was not associated with the initial specimens on which this genus was named. Thus, it was assumed that *Monstrocrinus* was a stemless crinoid that sat directly on the sea floor and, when alive, rolled around on its spines. For a variety of reasons, this seems unlikely, but the rolling crinoid lifestyle interpretation has persisted in the literature. More thorough cleaning of historical specimens and, more importantly, a new specimen with an attached column clearly refute the classical lifestyle interpretation and demonstrate that *Monstrocrinus* was a typical crinoid attached to a long column that was presumably anchored to the sea floor. In addition to revising the lifestyle of this crinoid, the varieties of spine types are redefined with names that more accurately reflect their morphology. *Monstrocrinus* occurs in Europe and South America, and one previously described species is placed in synonymy so that the genus is now comprised of three species.

Abstract.—The diplobathrid camerate crinoid genus *Monstrocrinus* is morphologically reinterpreted on the basis of new finds from the upper Emsian (Lower Devonian) to lower Eifelian (Middle Devonian) of Germany (Rhenish Slate Mountains, North Rhine-Westphalia, and Rhineland-Palatinate). The most complete, new specimen has a long segment of column projecting outward from the basal concavity, which confirms that the *Monstrocrinus* crown was attached to a column as an adult. Thus, a free-living life mode of a passively rolling or drifting crinoid is refuted and *Monstrocrinus* is reinterpreted as an attached, stalked echinoderm. This finding is supported by re-examination of the historical type material. A column attachment with a central pentalobate axial canal was recognized for the first time in the calyx of the holotype of the type species *Monstrocrinus securifer*. The holotype of *Monstrocrinus granosus* is far more complete than previously thought. It is a partially disarticulated crown embedded together with an associated longer part of the column. The extraordinary spines on the calyx plates of *Monstrocrinus* can be divided into eight morphological types and into two superordinate categories: “Category A” is a physical part of the calyx plate, whereas “Category B” is an attachment onto the calyx plate. Taxonomically, *M. aliformis* from the upper Emsian of Spain is treated herein as a subjective junior synonym of *M. securifer*.

Introduction

The historical type localities of numerous crinoid faunas in the Devonian of the Rhenish Slate Mountains are from distinct depositional facies. During the Early Devonian (late Siegenian [late Pragian] to the end of the early Emsian) ~70 crinoid species assigned to 28 genera are known from the famous “Hunsrückschiefer,” exposed between Koblenz, Trier, and Mainz (Bartels et al., 1998; Hess, 1999; Südkamp, 2017). Characteristic pyritized fossils of four primary crinoid clades are

represented by the genera *Codiacrinus* Schultze, 1866; *Imitatorcrinus* Schmidt, 1934; and *Parisangulocrinus* Schmidt, 1934 (Eucladida); *Calycanthocrinus* Follmann, 1887; and *Triacrinus* Münster, 1839 (Disparida); *Hapalocrinus* Jaekel, 1895; and *Thallocrinus* Jaekel, 1895 (Camerata); and *Eutaxocrinus* Springer, 1906 (Flexibilia).

The crinoids of the sandy Lower Devonian up to the *Cultrijugatus* Zone, which were summarized by Schmidt (1941), are the second important regional crinoid fauna. They occur at numerous localities along the western and eastern Rhenish Massif in a time slice between the late Siegenian (respectively late Pragian) to the early Eifelian. One hundred and twenty-five species assigned to 34 genera are discussed in this classic

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monograph, with most specimens preserved as hollow molds. Especially characteristic are the camerate genera *Ctenocrinus* Bronn, 1840; *Acanthocrinus* Roemer, 1850; *Monstrocrinus* Schmidt, 1941; and *Orthocrinus* Jaekel, 1895; as well as the eucladid *Eifelocrinus* Wanner, 1916 (see Bohatý, 2009, p. 195). *Monstrocrinus*, *Orthocrinus*, and *Eifelocrinus* also dominate the crinoid fauna of the Emsian–Eifelian boundary within the Rhenish Massif (Bohatý, 2009, p. 195). This boundary is characterized by the sedimentological change from the sandy sedimentation of the Emsian to the carbonate sedimentation of the Middle Devonian, which is associated with the establishment of extensive reefoid formation during the beginning of the Eifelian (Bohatý, 2009). This change also meant that the Emsian crinoid soft-bottom dwellers were increasingly associated with hard- and firmground dwellers. *Monstrocrinus*, *Orthocrinus*, and *Eifelocrinus* characterize a crinoid transitional fauna between the Lower and Middle Devonian facies realms, which locally only had a short stratigraphic range.

Supraregionally, *Monstrocrinus* is the youngest representative of the three genera mentioned with occurrences extending into the middle to upper Eifelian in Brazil, where the genus has the youngest known stratigraphic occurrence (Scheffler et al., 2006, 2011). *Monstrocrinus* is an enigmatic crinoid with long, elaborate spines attached to numerous calyx plates. Most preserved remains of this crinoid are isolated spines; thus, spine morphology has largely been the basis for species differentiation. Also, because neither an associated column nor a preserved external view of the infrabasal circler were known previously, a free-living benthic lifestyle was proposed for this unusual crinoid (e.g., Schmidt, 1941; Ettensohn, 1984). The new partially articulated specimens reported here with variable spine shapes on a single individual and an attached column allow a reassessment of *Monstrocrinus* systematics and paleoecology.

Location and stratigraphy

In the present work, new specimens of the spectacular, if enigmatic, *Monstrocrinus* are described from the uppermost Lower to Middle Devonian rocks of the Rhenish Slate Mountains (North Rhine-Westphalia and Rhineland-Palatinate, Germany; Fig. 1), which allow important insights into the mode of life and the functional morphology of this unusual crinoid. The material comes from the uppermost section of the Emsian *Orthocrinus* Beds (*Polygnathus costatus patulus* Conodont Biozone) of the locus typicus of the type species *Monstrocrinus securifer* Schmidt, 1941, at the former brickworks mine (slopes north, east, and south of the former brick factory, UTM: 51° 02'22.73"N, 7°51'51.02"E) in the Osterbachtal on today's federal road B54, northwest of Olpe-Lütringhausen (administrative district Arnsberg, Sauerland, North Rhine–Westphalia). The classic site is located at the southeastern flank of the Middle Devonian Attendorn–Elspe Double-Syncline in the transition to the Lower Devonian Siegen Anticline. Additional material is from two outcrops within the Eifel synclines. The first locality is the northern embankment at the “Eschfelder Seifen” on the southwestern flank of the Middle Devonian Ahrdorf Syncline, in the transition area to the Lower Devonian Wiesbaum Anticline (southeast of Dollendorf, NNW of Leudersdorf, North

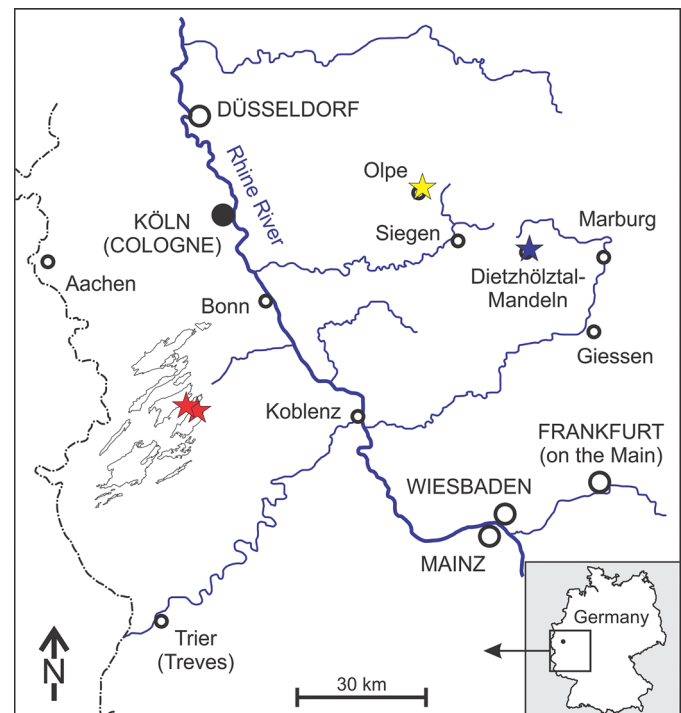


Figure 1. Geographical overview of the Rhenish Massif (modified from Korn, 2008, after Walter, 1995). The German *Monstrocrinus* localities are marked with stars: red stars mark the sites within the Eifel synclines (“Eschfelder Seifen,” in the west, and northern Ahabach Valley, in the east); the yellow star indicates the fossil locality in the Sauerland (former brick factory in the Osterbachtal); and the blue star marks the fossil site within the Lahn–Dill district (“Old Municipality Quarry” in Dietzhöhlztal–Mandeln).

Rhine–Westphalia; UTM: 50°21'45.62"N, 6°43'44.14"E). The second location is in the northern Ahabach Valley, on the north-northeastern flank of the Middle Devonian Hillesheim Syncline, in the transition area to the Lower Devonian Hoffeld Anticline (north-northeast of Üxheim–Ahütte, Rhineland–Palatinate; UTM: 50°20'56.25"N, 6°46'35.71"E). Stratigraphically, this material is from the Eifel synclines in the Lauch Formation (*Polygnathus costatus partitus* to lowermost *P. costatus costatus* Conodont biozones) of the lower Eifelian and, therefore, are somewhat younger than those from the Sauerland type locality north of Olpe.

Whereas the type species *Monstrocrinus securifer* Schmidt, 1941, is the only recorded *Monstrocrinus* to date within the Eifel, both species known in Germany occur together within the Emsian *Orthocrinus* Beds (*Polygnathus costatus patulus* Conodont Biozone) in the Sauerland (Olpe). However, *Monstrocrinus granosus* Schmidt, 1941, already occurs within the upper Emsian Mandeln Formation (*Polygnathus serotinus* Conodont Biozone) of Dietzhöhlztal–Mandeln in the Lahn–Dill district in central Hesse, north-northeast of Dillenburg (type locality at UTM: 50°51'22.52"N, 8°20'51.41"E).

Materials and methods

The majority of the *Monstrocrinus* specimens from the historic *M. securifer* type locality within the Sauerland (Olpe) and the *M. granosus* type locality within the Lahn–Dill district in Hesse (Dietzhöhlztal–Mandeln) are preserved as molds, which has

historically led to misinterpretations of *Monstrocrinus* morphology. For this study, some new preparation work was carried out on the holotypes of both species in order to be able to create new latex molds. These were whitened and digitally photographed with low-angle lighting. The new finds from the lower Eifelian of the Eifel synclines are in calcite preservation. These specimens were mechanically dissected using preparatory needles, micro sand-streaming methods, and fine pneumatic probes.

Repositories and institutional abbreviations.—The original material of *Monstrocrinus securifer* is deposited with the abbreviation IGPB in the Steinmann Institute for Geology, Mineralogy, and Paleontology of the Rhenish Friedrich Wilhelm University of Bonn, Germany. The type material of *M. granosus* is deposited with the abbreviation SMF in the Senckenberg Research Institute and Natural History Museum Frankfurt on the Main, Germany. Specimen no. NHMMZ PWL 2021/6145-LS is deposited in the State Collection of Natural History of Rhineland–Palatinate at the Natural History Museum Mainz (NHMMZ), Germany. The type material of *M. incognitus* is housed in the paleontological collection of the Departamento de Geologia e Paleontologia do Museu Nacional, Universidade Federal do Rio de Janeiro (UFRJ), Brazil, under institutional abbreviation no. MN8277-Id. (holotype) and nos. MN8277-Ia, and MN8277-Ib (paratypes).

Systematic paleontology

The superfamilial classification used here follows Cole (2017), Wright (2017), and Wright et al. (2017). Family-level classifications follow Moore and Teichert (1978). Morphologic terminology follows Webster (1974), Ubaghs (1978a), Ausich et al. (2020), and Ausich and Donovan (2023). The plating of interrays is given by the number of plates in each range from proximalmost plate to the last range before the tegmen. In the posterior interray, the primanal is indicated by “P;” and in regular interrays, the first interradial plate is indicated by “1.” A “?” indicates that more distal plating is unknown (Ausich, 2021). Abbreviations used in designating measurements include: CrH, crown height; CaH, calyx height; CaW, calyx width; CoH, column height. An asterisk (“*”) indicates an incomplete measurement.

Class Crinoidea Miller, 1821
Subclass Camerata Wachsmuth and Springer, 1885
Infraclass Eucamerata Cole, 2017
Order Diplobathrida Moore and Laudon, 1943
Superfamily Rhodocrinitoidea Roemer, 1855
Family Rhodocrinitidae Roemer, 1855
Genus *Monstrocrinus* Schmidt, 1941

Type species.—*Monstrocrinus securifer* Schmidt, 1941.

Other species.—*Monstrocrinus granosus* Schmidt, 1941; and *M. incognitus* Scheffler et al., 2011.

Emended diagnosis.—Rhodocrinitid with a medium bowl- to globe-shaped calyx, distal corners of infrabasal plates not visible in lateral view, proximal regular interrays with 1–3

plating, proximal CD interrays with 1–3 plating, median ray ridges absent, anitaxial ridge absent, primaxil hexagonal, calyx plates with various types of long spines attached to calyx plates, fixed pinnules absent, 20(?) free arms that divide once, brachials chisel biserial.

Occurrence.—Upper Emsian (Lower Devonian) to lower Eifelian (Middle Devonian) of Europe (Rhenish Slate Mountains, North Rhine-Westphalia, Rhineland-Palatinate, and Hesse, Germany; and province of Teruel, Aragon, Spain). Middle and upper Eifelian (Middle Devonian) of South America (states of Pará and Tocantins, Brazil) (Ferreira and Fernandes, 1989; Fernandes et al., 2000; Scheffler et al., 2006, 2009, 2011, 2015; Gama Jr. and Scheffler, 2007; Scheffler, 2010, 2015). The occurrence of the genus *Monstrocrinus* in the Emsian–Eifelian boundary interval of the lowermost part of the Chefar El Ahmar Formation of the Ougarta Mountains in the Sahara province of Béni Abbès in southwestern Algeria in the Maghreb region of North Africa (see Le Menn, 1990, 1997) is not proven taxonomically.

Remarks.—In addition to complete specimens of *Orthocrinus tuberculatus* Schmidt, 1913, and *Arthroacantha* Williams, 1883, Schmidt (1924, p. 17) mentioned a new crinoid genus “with unusually monstrous, axe-shaped spines on the basals and radials” from the former brickworks mine in the Osterbachtal, northwest of Olpe-Lütringhausen (see “Location and stratigraphy”). Seventeen years later, Schmidt (1941, p. 213–215) described this as *Monstrocrinus* n. gen. and considered this new discovery to have been a free-living benthic rhodocrinitid genus, which is characterized by “monstrous floating spines” (he interpreted the paddle-like, equatorially projecting spiny appendages of the calyx as useful elements for passive drifting on the sea bottom; see Fig. 2.3) and “very flexible, two-lined arms.” However, he pointed out that the genus was incompletely known and required a full description (Schmidt, 1941, p. 213). His diagnosis was based on various disarticulated plates of the calyx as well as remains of the “floating spines.” This material was from different specimens and localities, which systematically cannot be assigned unequivocally to a genus or to one of the two *Monstrocrinus* species described by him. Nevertheless, Schmidt (1941, p. 213) combined these individual parts into a genus and species description. In addition, Schmidt (1941, p. 213) justified the lack of a stem with the alleged lack of a “stem scar” on the aboral side of the calyx; the column lumen was said to be closed by the fact that the proximal plates of the calyx are supposed to have grown together until the “column hole” was completely closed (Schmidt, 1941, p. 215). The inconclusive evidence for this is a gelatin cast of the interior of a single calyx remnant preserved as a mold and required a full description (Schmidt, 1941, p. 216). However, our re-examination of the type material revealed that this assumption was incorrect. Furthermore, Schmidt (1941, p. 215) deduced from disarticulated arm remains of his type specimen for *M. granosus* that the arms of all *Monstrocrinus* species must have been relatively short.

The type species, *Monstrocrinus securifer* Schmidt, 1941, p. 215–217, was described as a large representative of the

genus, which was characterized by vertically positioned, axe-shaped “floating spines.” The surface of the crown ossicles is unornamented. The specimens described by Schmidt (1941) are from the uppermost section of the Emsian *Orthocrinus* Beds in the area around Olpe; these are: (1) the former brickworks mine NW of Olpe-Lütringhausen (see Location and stratigraphy); (2) the abandoned “Waukemicke Quarry” (Olpe-Waukemicke); (3) several fossil localities near Olpe-Oberveischede; and (4) the fossil localities at the “Siele Farmyard” (between Olpe-Lütringhausen and Olpe-Waukemicke). Schmidt also mentioned *M. securifer* remains from localities outside Olpe (Bad Laasphe–Feudingen in the Siegen–Wittgenstein district in North Rhine-Westphalia and the “Old Paper Mill Haiger Hut,” NE-Haiger in the northern part of the Lahn–Dill district in central Hesse).

The second species, *M. granosus* Schmidt, 1941, p. 217–218, was described as a medium-sized species that is characterized by a granular ornamentation of the calyx, by single-pointed and forked “floating spines,” and by “two-lined arms.” The species occurs in the upper Emsian Mandeln Formation within the “iron-shed greywacke schist” in the “Old Municipality Quarry” at the northern Hauberg Hill in Dietzhöhlztal–Mandeln in the Lahn–Dill district in central Hesse, north-northeast of Dillenburg. The original material was discovered by the late geologist Gerhard Solle (1911–1981), who found the specimen in 1935. It is deposited in the Senckenberg Research Institute and Natural History Museum Frankfurt under catalog number SMF-XXIII-113a. Forty-three years later Ettensohn (1984) discussed genus *Monstrocrinus* as a stemless crinoid genus that was passively moved by current.

Le Menn (1990) described an isolated plate with preserved appendages from the upper Emsian Pena Negra Formation northeast of the municipality of Loscos in the province of Teruel, Aragon, Spain (Le Menn, 1990, p. 151–153). This specimen has a striking elk-antler-like morphology (Le Menn, 1990, p. 152, figs. 1a, b; see Fig. 3.3). This extreme morphology was considered distinct from the “floating spines” of the type species, *M. securifer*, described by Schmidt (1941). Thus, Le Menn (1990) described the new species *M. aliformis* Le Menn, 1990. However, new specimens of *M. securifer* described herein from the lowermost Eifelian of the Ahrdorf- and Hillesheim Eifel synclines demonstrate that the spine morphology of *M. aliformis* falls within the range of variation of the spine processes of *M. securifer*. Therefore, *M. aliformis* is treated herein as a subjective junior synonym of *M. securifer*. These new specimens also have an effect on our understanding of the evolutionary development of the “floating spines” as postulated by Le Menn (1990, p. 156, fig. 3). According to Le Menn’s model, the tapering *Acanthocrinus* spines (1990, p. 156, fig. 3a) were first modified to form the forked *Monstrocrinus granosus* spines (Le Menn, 1990, p. 156, fig. 3b; see Fig. 3.2), which then became the elk-antler-like spines of the species *M. aliformis* (Le Menn, 1990, p. 156, fig. 3c, see Fig. 3.3), and finally adopted the “paddle-like floating prong shape” of the species *M. securifer* (Le Menn, 1990, p. 156, fig. 3d). This development was said to have taken place between the lower to the uppermost Emsian. Beside the fact that the *M. granosus* spine shown in Schmidt (1941, p. 217, fig. 61, no. b2) has no particular taxonomic relevance, it was wrongly interpreted by Le Menn

(1990, p. 156, fig. 3b). The prong-shaped extension (Fig. 3.2) was interpreted as pointing to the calyx plate (proximally). However, it is not a backward-pointing prong but a distally tapering bifurcation (cf., Schmidt, 1941, p. 217). The proposed evolutionary model is furthermore refuted by the common occurrence of different forms of spinous calyx plate appendages of all *Monstrocrinus* species.

Furthermore, Le Menn (1990, p. 152, figs. 1c, d) figured two isolated calyx plates with narrow appendages as *Monstrocrinus* sp. from Emsian–Eifelian boundary of the lowermost part of the Chefar El Ahmar Formation of the Ougarta Mountains in the Sahara province of Béni Abbès in southwestern Algeria (also illustrated in Le Menn, 1997, pl. 4, fig. 14). The plate fragment (Fig. 3.4) shown in Le Menn (1990, p. 152, figs. 1c, d) cannot be clearly assigned to the genus *Monstrocrinus*. Le Menn postulated that *Monstrocrinus* was stratigraphically restricted to the upper Emsian and that none of the species crossed the Lower–Middle Devonian boundary (Le Menn, 1990, p. 149–150), which is refuted by specimens from the Lauch Formation of the lower Eifelian of the Eifel synclines and by the *Monstrocrinus* discoveries from the Eifelian strata of Brazil (see below).

Scheffler et al. (2006) described “*Monstrocrinus securifer*” from the middle Eifelian Maecuru Formation along the Maecuru River in the northwestern part of the State of Pará in Brazil. In addition to the characteristic “floating spines,” the authors also depicted an *Acanthocrinus*-like spine for the first time and assigned it to “*M. securifer*” (Scheffler et al., 2006, p. 238, fig. 3E). This isolated calyx plate can only be assigned to the genus *Monstrocrinus* with reservation because numerous members of the family Rhodocrinitidae Roemer, 1855, have similar plates. Nevertheless, the articulated specimen described in the present work proves that *Monstrocrinus* had *Acanthocrinus*-like spines in addition to differently designed “floating spines.”

Scheffler et al. (2009) described additional remains of the calyx and crown of the genus *Monstrocrinus* and stated that each arm divided twice, resulting in four free arms per ray. Scheffler et al. (2011) erected the new species *Monstrocrinus incognitus* from the middle to upper Eifelian Pimenteira Formation of the Parnaíba Basin in the State of Estado do Tocantins in Brazil. To date, this is the youngest species of the genus and was considered an intermediate form between “*M. securifer*” (with regard to the “floating spines” of Scheffler et al., 2006, identified from the Maecuru Formation in Brazil) and “*M. aliformis*” from the Pena Negra formation of Spain (Scheffler et al., 2011, p. 1189). In contrast to these species, the “floating spines” should be characterized by short webs between the calyx plate attachment and the distal “wings” as well as by distally widened “wing appendages.” Note that the incomplete calyx plate in Scheffler et al. (2011, p. 1192, fig. 4.2) has a longer web between the base of the plate and the distal “wing end” in comparison with the other examples illustrated (Scheffler et al., 2011, p. 1192, figs. 4.1, 4.3–4.6). This could indicate an insufficiently recorded morphological variability, as demonstrated for the type species in the present work. According to Scheffler et al. (2011, p. 1192), the widened outer edge of the distal “floating spines” could have been useful for both an increase in the water turbulence in the direction of the arms in the parabolic filter position and for anchoring on the substrate (Scheffler et al., 2011, p. 1197).

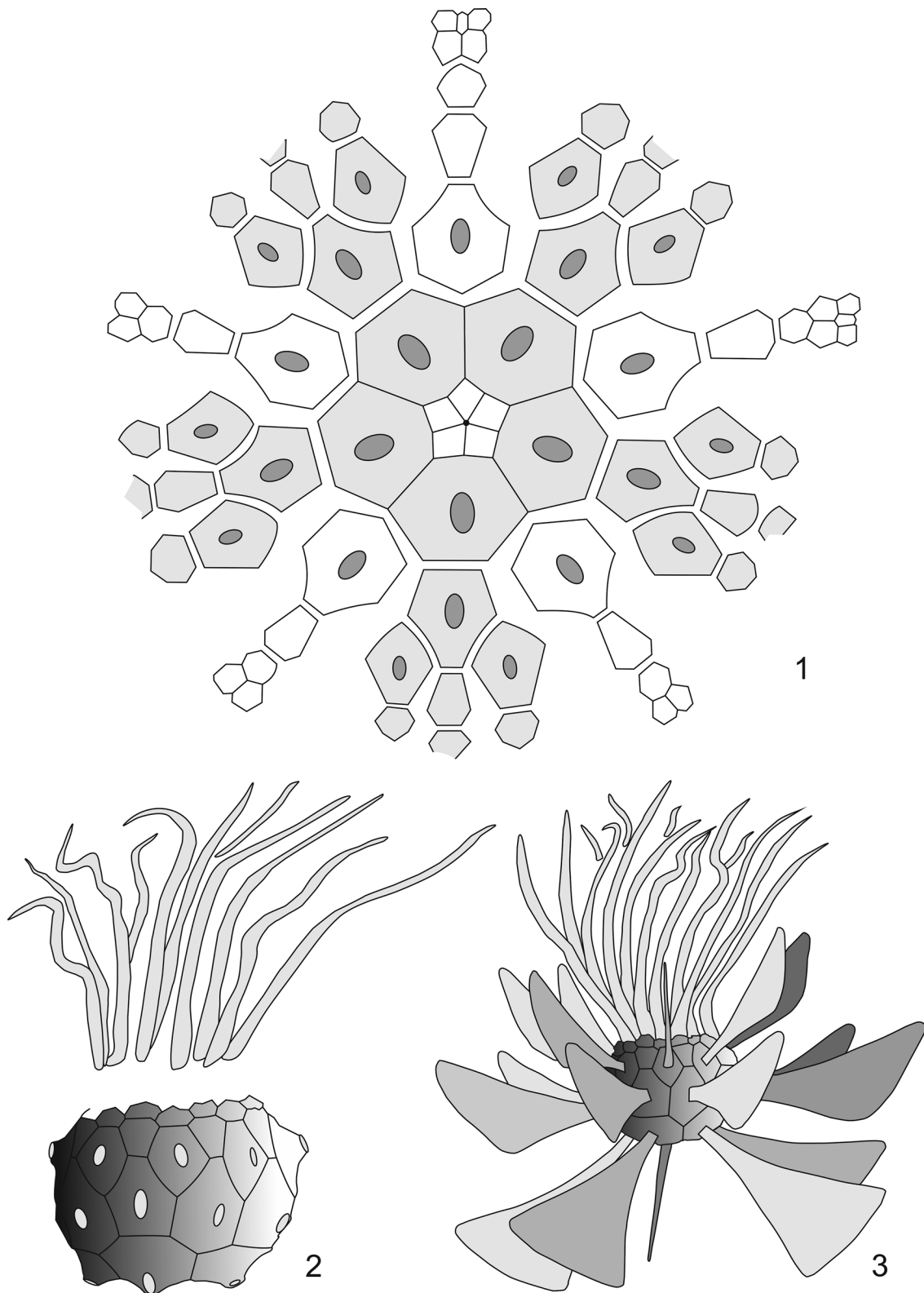


Figure 2. (1) Calyx plate diagram of *Monstrocrinus securifer* according to Schmidt (1941, p. 214, Fig. 60a). (2) Schematic reconstruction drawing of a *Monstrocrinus* calyx with “broken off floating spines” and “indicated arms” after Schmidt (1941, p. 214, Fig. 60b). (3) Reconstruction drawing of *Monstrocrinus securifer*, previously interpreted as a stemless crinoid, with “completely preserved floating spines” (after Schmidt, 1941, p. 214, Fig. 60b); arms are simplified.

The first two steps toward an understanding of *Monstrocrinus* is a standardized method for describing calyx spines, which then allows a means to describe spine variability more precisely

on a single individual, from a single fossiliferous horizon, and intra- and interspecific variability. Figure 4 is a model for description of calyx spine shapes that builds on Scheffler et al.

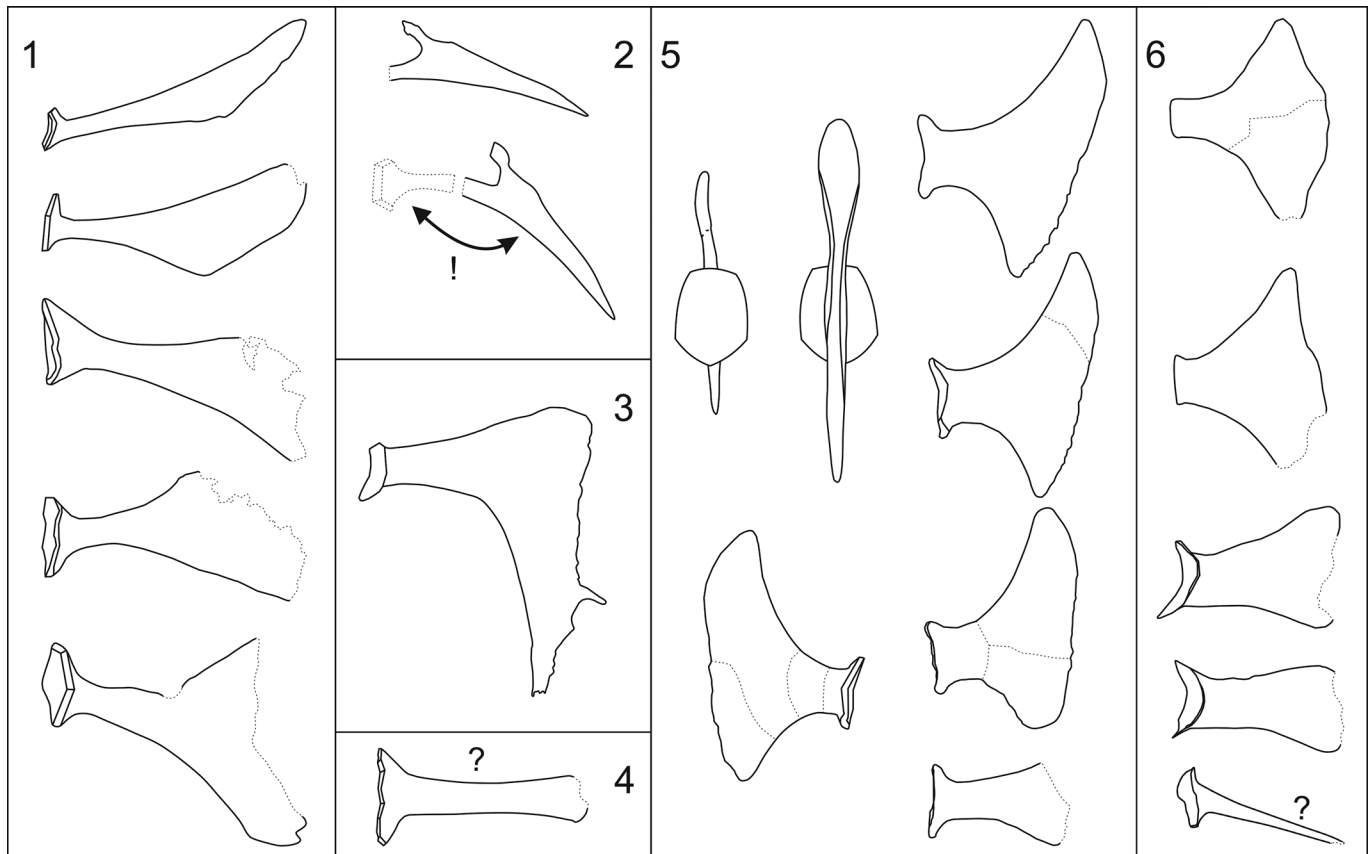


Figure 3. The isolated spiny calyx plate appendages of genus *Monstrocrinus* depicted in the literature. (1) *Monstrocrinus securifer* (after Schmidt, 1941, pl. 16). (2) *Monstrocrinus granosus* (after Schmidt, 1941, p. 217, fig. 61, no. b2), the upper figure shows a disarticulated distally forking spiny calyx plate appendage. Le Menn (1990, p. 156, fig. 3b) wrongly interpreted the prong-shaped extension as pointing proximally toward the calyx plate (see lower figure); however, the prong-shaped extension is not a backward-pointing prong, but a distally tapering bifurcation (see Schmidt, 1941, p. 217). (3) “*Monstrocrinus aliformis*” (after Le Menn, 1990, p. 152, fig. 1b). The species is interpreted in the present work as a subjective younger synonym of *M. securifer*. (4) “*Monstrocrinus* sp.” according to Le Menn (1990, p. 152, fig. 1d; 1997, pl. IV, fig. 14). The plate fragment cannot be clearly assigned to the genus *Monstrocrinus*. (5) *Monstrocrinus incognitus* (after Scheffler et al., 2011, p. 1191–1192, figs. 3, 4.1–4.6). (6) “*Monstrocrinus securifer*” (after Scheffler et al., 2006, p. 238, fig. 3A–3E), either belonging to *M. incognitus* or to another species (further investigations are needed). The isolated spine shown at the bottom of the figure cannot be unequivocally assigned to the genus *Monstrocrinus*.

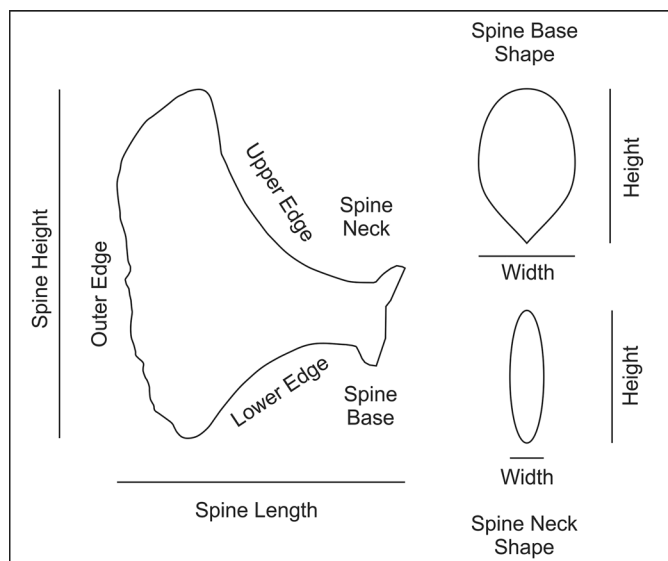


Figure 4. Morphological features of *Monstrocrinus* spines (modified from Scheffler et al., 2011, p. 1191, fig. 3).

(2011, fig. 3). The height and width of the entire calyx spine can be measured. The spine base has an outline shape and a height and width. Similarly, the spine neck (immediately abaxial from the spine base) has a cross-sectional shape and a height and width. The remainder of the calyx spine is referred to as the spine blade. This is the highly variable portion of the spine. The shape of spines is largely a function of different shapes of the upper edge, external edge, and lower edge (Fig. 4).

There is a wide range of spine shapes in *Monstrocrinus*. Based on the examined fossil material it is now possible to distinguish eight standardized morphological spine types (Fig. 5). They are the following types:

Type 1: tapering, pointed spine.—Entire spine circular to subcircular in cross section; tapers to a point at terminus (Figs. 6.2, 9.2, 10, 12.1, 12.3, 12.4).

Type 2: blunt spine.—Entire spine higher than wide, elliptical in cross section; upper and lower edges either slightly expanding, parallel, or slightly narrowing; tapers to a flat, blunt terminus (Fig. 9.2).

Category	Definition of standardized morphological calyx spine types 1-8	* <i>M. securifer</i>	<i>M. granosus</i>	<i>M. incognitus</i>
Category A	Type 1	X	X	X
	Type 2		X	
Category B	Type 3	X		
	Type 4 (Subtypes 4a-4b)	X		X
	Type 5 (Subtypes 5a-5b)			X
	Type 6	X	X	
	Type 7	X	X	
	Type 8	X		

Figure 5. Categorization of transitions between calyx plate and spine and definition of standardized morphological calyx spine types and subtypes.

Type 3: narrow paddle-shaped spine.—Neck long, much higher than wide, flat ellipse in cross section, gradually increases in height toward outer edge; upper and lower edges concave; entire spine expands gradually toward outer edge, lower edge longer, strongly asymmetrical; outer edge at an acute angle to horizontal; smooth or serrated (Fig. 8.1–8.3).

Type 4: broad paddle-shaped spine.—Neck short, much higher than wide, flat ellipse in cross section, rapidly increases in height toward outer edge; upper and lower edges sharply concave; entire spine expands rapidly in height, upper and lower edges very convex and expand at different rates yielding an asymmetrical spine; outer edge at a high angle to horizontal; straight or broadly convex; smooth or serrated. Type 4 spine shapes can be subdivided into two subtypes: (1) subtype 4a—upper edge longer and higher, spine asymmetrical upward; and (2) subtype 4b—lower edge longer and lower, spine asymmetrical downward (Fig. 8.4).

Type 5: flat, high fan.—Neck variable in shape, much higher than wide, flat ellipse in cross section; upper and lower edges parallel or broadly concave; entire spine shape variable; outer edge at high angle to horizontal, smooth. Type 5 spine shapes can be subdivided into two subtypes: (1) subtype 5a—neck short; upper and lower edges broadly concave, entire spine relatively short, gradually expanding in height toward outer edge; outer edge broadly convex; and subtype 5b—neck long, short, or undifferentiated; upper and lower edges very broadly concave or subparallel; entire spine gradually expanding from the neck, shortest at mid-spine position, or rectilinear; outer edge concave with or without upper and lower blunt extensions.

Type 6: bifurcating spine.—Neck long or short, much higher than wide, flat ellipse in cross section; entire fan gradually expanding in height toward outer edge, upper and lower edges broadly concave, bifurcates into two spines near or away from the spine base, entire spine symmetrical or asymmetrical; terminal extensions circular to subcircular in cross section, taper to a blunt point (Figs. 8.5, 12.2).

Type 7: forked spine.—Neck of various lengths, much higher than wide, flat ellipse in cross section; entire spine gradually

expanding in height toward outer edge, upper and lower edges broadly concave; outer margin with various spine sizes and arrangements, spines may be long or short, may assume a serrated appearance, are arranged symmetrically or asymmetrically; spine cross section circular to elliptical. (Figs. 8.6, 8.7, 9.2, 10, 12.2, 12.4).

Type 8: strongly asymmetrical paddle shaped spine with spinose outer margin.—Neck short, much higher than wide, flat ellipse in cross section, rapidly increases in height toward outer edge; entire spine with upper and lower edges concave, expanding in height distally, lower edge more convex, longer, and lower; highly asymmetrical; outer edge at a high angle to horizontal, straight or broadly concave, serrated or with small spines (Fig. 8.8, 8.9).

These eight morphological types can be divided into two additional categories (Category A and B), because calyxes of *Monstrocrinus* have two different types of transitions between the proximally positioned calyx plate and the distally projecting end of the spine. Category A is a spine that truly seems to be completely a physical part of the calyx plate, whereas Category B appears to be an attachment onto the calyx plate, which is either positioned immediately proximal to a more planar calyx plate (e.g., in *M. granosus*), or somewhat higher, at the distal end of a funnel-shaped calyx plate projecting externally (e.g., in *M. securifer*; see Fig. 8.10–8.12). In *M. granosus*, the outer portion of the calyx plate is coarsely granulated, whereas the center of the plate has much less granulation. Here it seems that both the spine and spinous process were able to detach immediately from the flat and heavily granulated calyx plate. Category B possibly can be interpreted as a kind of “secondary spine.” Category A can be observed in morphological spine Types 1 and 2, and category B occurs in Types 3–8.

This standardized typing and categorization, which is distributed among the examined *Monstrocrinus* species as shown in Figure 5, enables the subsequent differential diagnosis of the individual *Monstrocrinus* species. Species-diagnostic characters include the relative size of the calyx, calyx plate sculpturing, presence, or absence of depressions at calyx plate triple junctions, spine categories, and spine types.

Monstrocrinus securifer Schmidt, 1941

Figures 2, 3.1, 3.3, 6–8

1941 *Monstrocrinus securifer* Schmidt, p. 214–217, fig. 60a–c, pl. 16, figs. 1–7.

1978b *Monstrocrinus securifer*; Ubaghs, p. T428, T429, fig. 237a, b.

1990 *Monstrocrinus securifer*; Le Menn, p. 156, fig. 3d.

1990 *Monstrocrinus aliformis* Le Menn, p. 151–153, 156, figs. 1a, b, 3c.

2012 *Monstrocrinus securifer*; Hauser, p. 1–4, text-figs. 4–6 (non text-fig 3).

non *Monstrocrinus granosus* or *Acanthocrinus* sp.; Hauser, p. 4, text-fig. 6, no. 2a (= holotype of *M. securifer*).

Types.—Holotype: mold of an isolated calyx with rudimentarily preserved spines in matrix, no. IGPB-SCHMIDT, W.E.-18a (recast and re-illustrated in Fig. 6), original of Schmidt (1941,

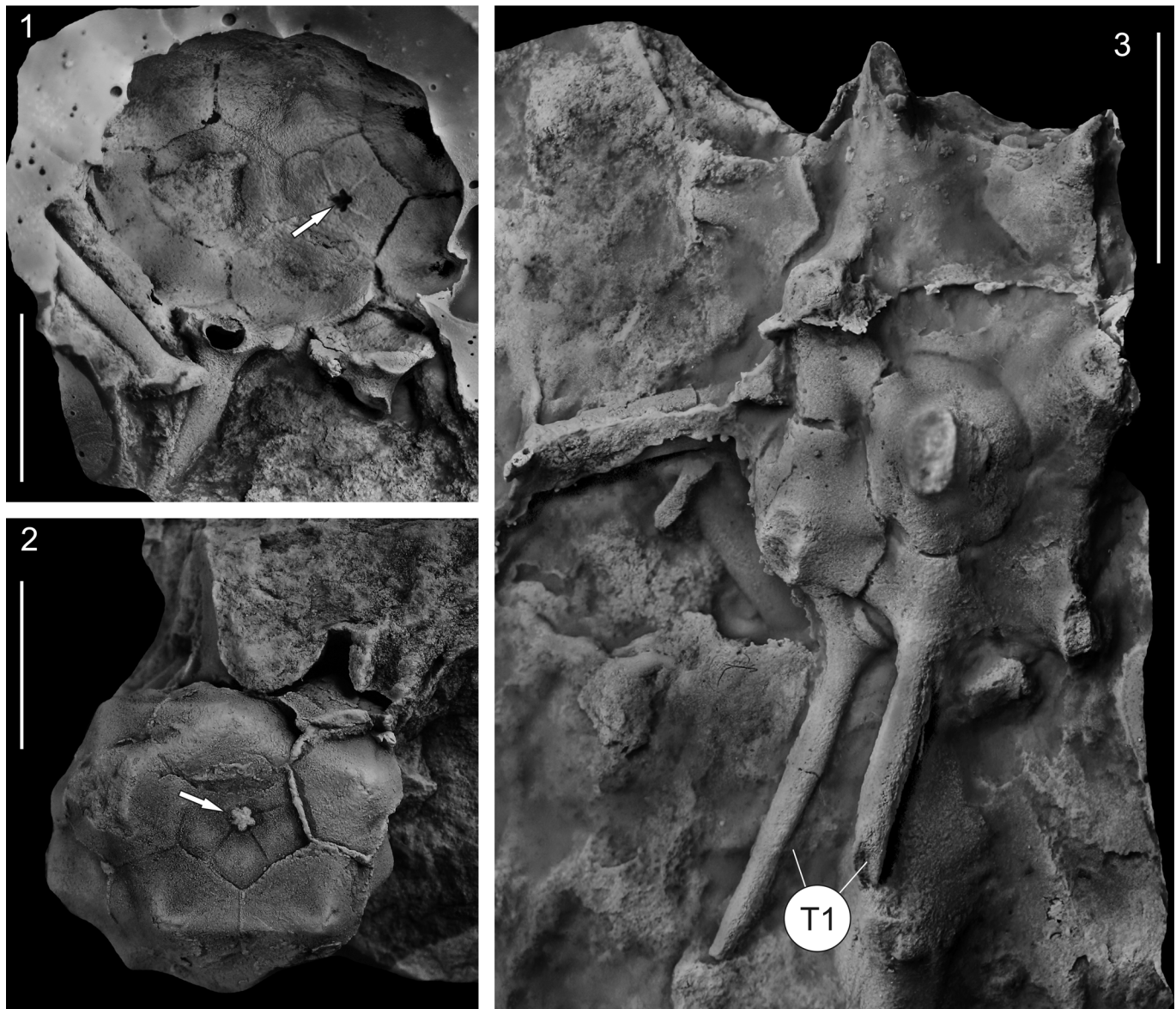


Figure 6. Recast holotype of *Monstrocrinus securifer* Schmidt, 1941 (no. IGPB-SCHMIDT, W.E.-18a) from the uppermost section of the Emsian *Orthocrinus* Beds (*Polygnathus costatus patulus* Conodont Biozone) of the former brick factory in the Osterbachtal, northwest of Olpe-Lütringhausen (administrative district Arnsberg, Sauerland, North Rhine–Westphalia, Germany). (1, 2) Aboral view of the calyx, showing pentalobate axial canal (white arrows), which were not shown in the original illustration by Schmidt (1941, pl. 16, fig. 2b); (3) lateral view of the calyx with rudimentarily preserved type 1 spines (white T1). Scale bars = 1 cm.

pl. 16, figs. 2a, b). Paratype: mold of an isolated base of a calyx in matrix, no. IGPB-SCHMIDT, W.E.-18c (recast and re-illustrated in Fig. 7), original of Schmidt (1941, pl. 16, fig. 3).

Emended diagnosis.—*Monstrocrinus* with a relatively large calyx, smooth plate sculpturing, shallow depressions at calyx plate triple junctions, spine categories (A, spine that is physically part of a calyx plate; B, spine articulated with calyx plate); spine types (1, tapering point; 3, narrow paddle shaped; 4, broad paddled shape; 6, bifurcating; 7, forked; 8, strongly asymmetrical with spines on outer margin).

Occurrence.—The locus typicus of *M. securifer* is the former brickworks mine (slopes north, east, and south of the former

brick factory, at UTM: 51°02'22.73"N, 7°51'51.02"E) in the Osterbachtal on today's federal road B54, northwest of Olpe-Lütringhausen (administrative district Arnsberg, Sauerland, North Rhine–Westphalia, Germany). The classic site is located at the southeastern flank of the Middle Devonian Attendorn–Elspe Double Syncline in the transition to the Lower Devonian Siegen Anticline and stratigraphically belongs to the uppermost section of the Emsian (Lower Devonian) *Orthocrinus* Beds (*Polygnathus costatus patulus* Conodont Biozone). Additional specimens described by Schmidt (1941) are from the abandoned “Waukemick Quarry” (Olpe-Waukemicke); from several fossil localities near Olpe-Oberveischede; and from the fossil localities at the “Siele Farmyard” (between Olpe-Lütringhausen and

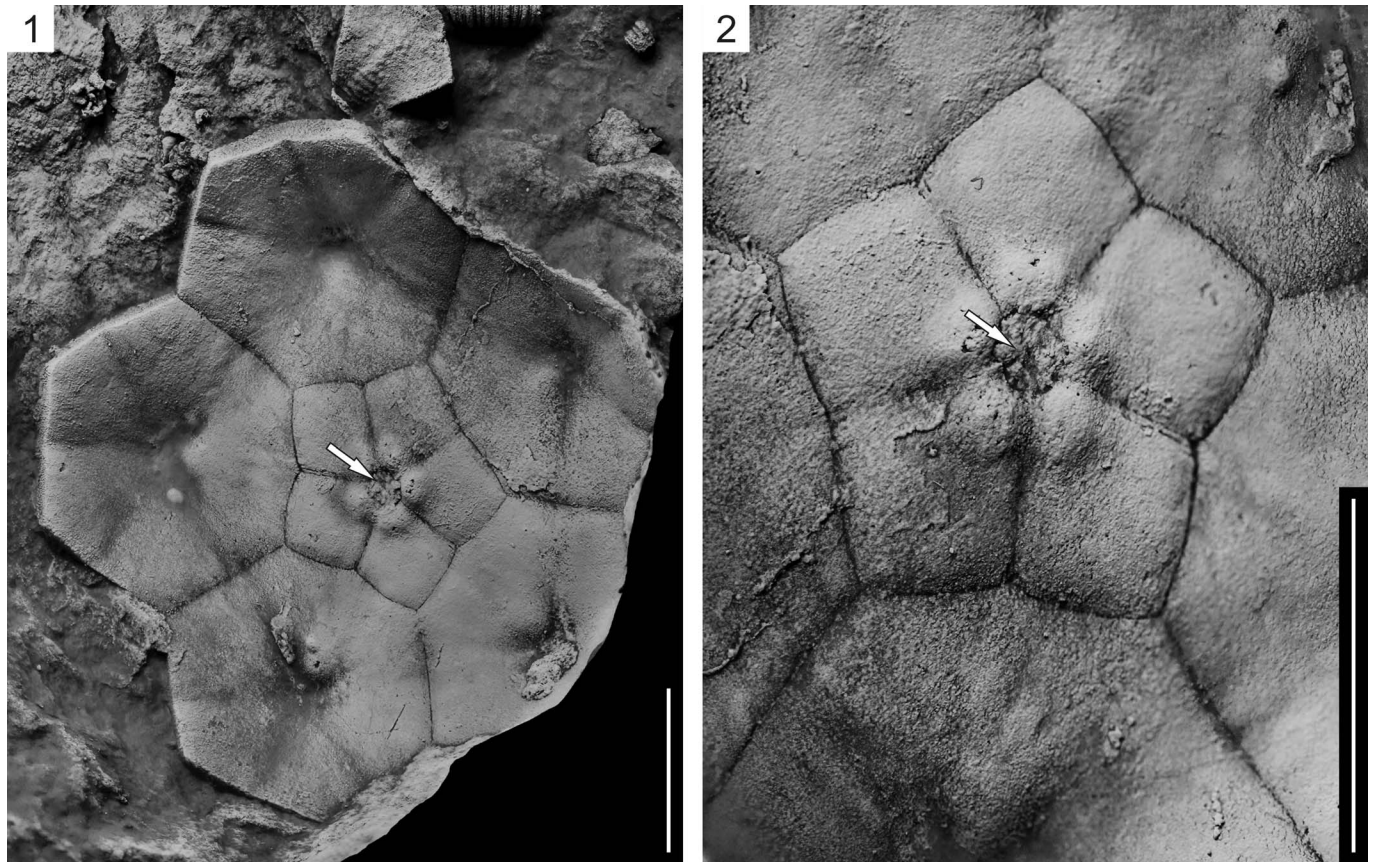


Figure 7. Recast paratype of *Monstrocrinus securifer* Schmidt, 1941 (no IGPB-SCHMIDT, W.E.-18c) from the uppermost section of the Emsian *Orthocrinus* Beds (*Polygnathus costatus patulus* Conodont Biozone) of the former brick factory in the Osterbachtal, northwest of Olpe-Lütringhausen (administrative district Arnsberg, Sauerland, North Rhine–Westphalia, Germany). (1, 2) Internal aboral view of isolated base of a calyx, showing narrow stem axial canal impression (white arrows), which Schmidt mistakenly interpreted as closed (see Schmidt, 1941, pl. 16, fig. 3). Scale bars = 1 cm.

Olpe-Waukemiecke). Schmidt also mentioned *M. securifer* remains from localities outside Olpe (Bad Laasphe–Feudinggen in the Siegen–Wittgenstein district in North Rhine–Westphalia and the “Old Paper Mill Haiger Hut,” NE-Haiger in the northern part of the Lahn–Dill district in central Hesse, Germany).

Additional material studied in the course of this work is from two outcrops within the Eifel synclines. The first locality is the northern embankment at the “Eschfelder Seifen” on the southwestern flank of the Middle Devonian Ahrdorf Syncline, in the transition area to the Lower Devonian Wiesbaum Anticline (southeast of Dollendorf, NNW of Leudersdorf, North Rhine–Westphalia; UTM: 50°21′45.62″N, 6°43′44.14″E). The second location is in the northern Ahabach Valley, on the north-northeastern flank of the Middle Devonian Hillesheim Syncline, in the transition area to the Lower Devonian Hoffeld Anticline (north-northeast of Üxheim–Ahütte, Rhineland–Palatinate; UTM: 50°20′56.25″N, 6°46′35.71″E) and stratigraphically belongs to the Lauch Formation (*Polygnathus costatus partitus* to lowermost *P. costatus costatus* Conodont biozones) of the lower Eifelian.

Because “*M. aliformis*” sensu Le Menn, 1990 is treated herein as a subjective junior synonym of *M. securifer*, the species also occurs in the upper Emsian part of the Pena Negra Formation, northeast of the municipality of Loscos in the province of Teruel, Aragon, Spain.

Emended description.—Calyx medium in size, medium to high globe-shaped calyx with a shallow basal concavity, calyx height:width ratio 1.25; depressions at calyx plate triple junctions present; plate sculpturing around spine bases smooth. Infrabasal plates confined to basal concavity, not visible in lateral view; five infrabasal plates. Five basal plates form part of calyx base and proximal portion of the calyx vertical wall. Radial circlet with ten plates (all radial plates alternate with interradial plates); presumably five radial plates, large, hexagonal, approximately as high as wide, with broad plications that connect to like plications on adjoining plates. Calyx plates with various long spines including spine categories A (spine that is physically part of a calyx plate) and B (spine articulated with calyx plate), and spine types 1 (tapering point), 3 (narrow paddle shaped), 4 (broad paddled shape), 6 (bifurcating), 7 (forked), and 8 (strongly asymmetrical with spines on outer margin). Proximal regular interradial plates large, approximately the same size as radial plates. First interradial plate higher than wide. CD interray not known. Fixed brachials present but the number is unknown, median ray ridges absent. Tegmen and free arms unknown. Column shape presumably circular, nodals wider than internodals, pentalobate lumen.

Remarks.—Re-examination of the historical type material of Schmidt (1941) revealed that the base of the calyx of

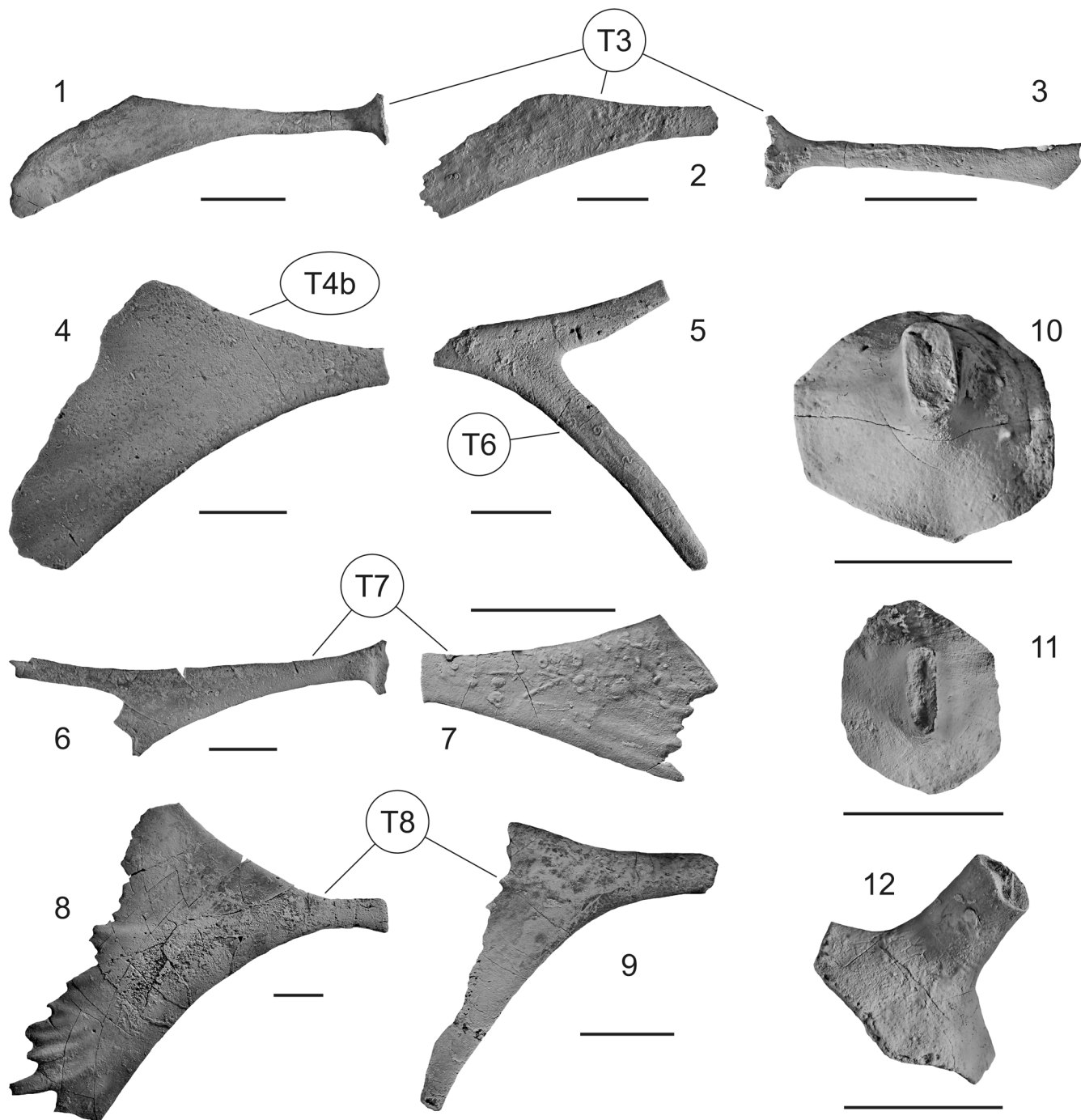


Figure 8. Calcite-preserved spines (1–9) and isolated calyx plates (10–12) of *Monstrocrinus securifer* Schmidt, 1941, from the Lauch Formation (*Polygnathus costatus partitus* to lowermost *P. costatus costatus* Conodont biozones) of the lower Eifelian of the Eifel synclines, Germany; (1, 4–12) are from the “Eschfelder Seifen,” southeast of Dollendorf, north-northwest of Leudersdorf, North Rhine–Westphalia; (2, 3) are from the northern Ahabach Valley, north-northeast of Üxheim–Ahütte, Rhineland–Palatine). (1–3) Type 3 spines (T3); (4) subtype 4b spine (T4b); (5) type 6 spine (T6); (6, 7) type 7 spines (T7); (8, 9) type 8 spines (T8); (10, 11) isolated calyx plates with “Category B” transitions between the proximally positioned calyx plates and the distally projecting end of the spines (“secondary spines,” not preserved). The spine attachment shows eight-shaped concavities. Scale bars = 1 cm.

Monstrocrinus securifer has a stem attachment with a central pentalobate axial canal, which confirms that the *M. securifer* crown was attached to a column as an adult (see Figs. 6.1, 6.3, 7). Thus, a free-living life mode of a passively rolling or drifting crinoid is refuted, and the type species is reinterpreted as an attached, stalked crinoid.

The longest spine of *M. securifer* examined by us is 7.5 cm long, with the base missing (Fig. 8.8). So, it was originally about 8.0 cm long. Our measurements show that the largest-known calyxes (without preserved spines) have at least 4.0 cm in equatorial cross-section. If this calyx is now placed between two of our approximately 8.0-cm long spines on the equatorial plane,

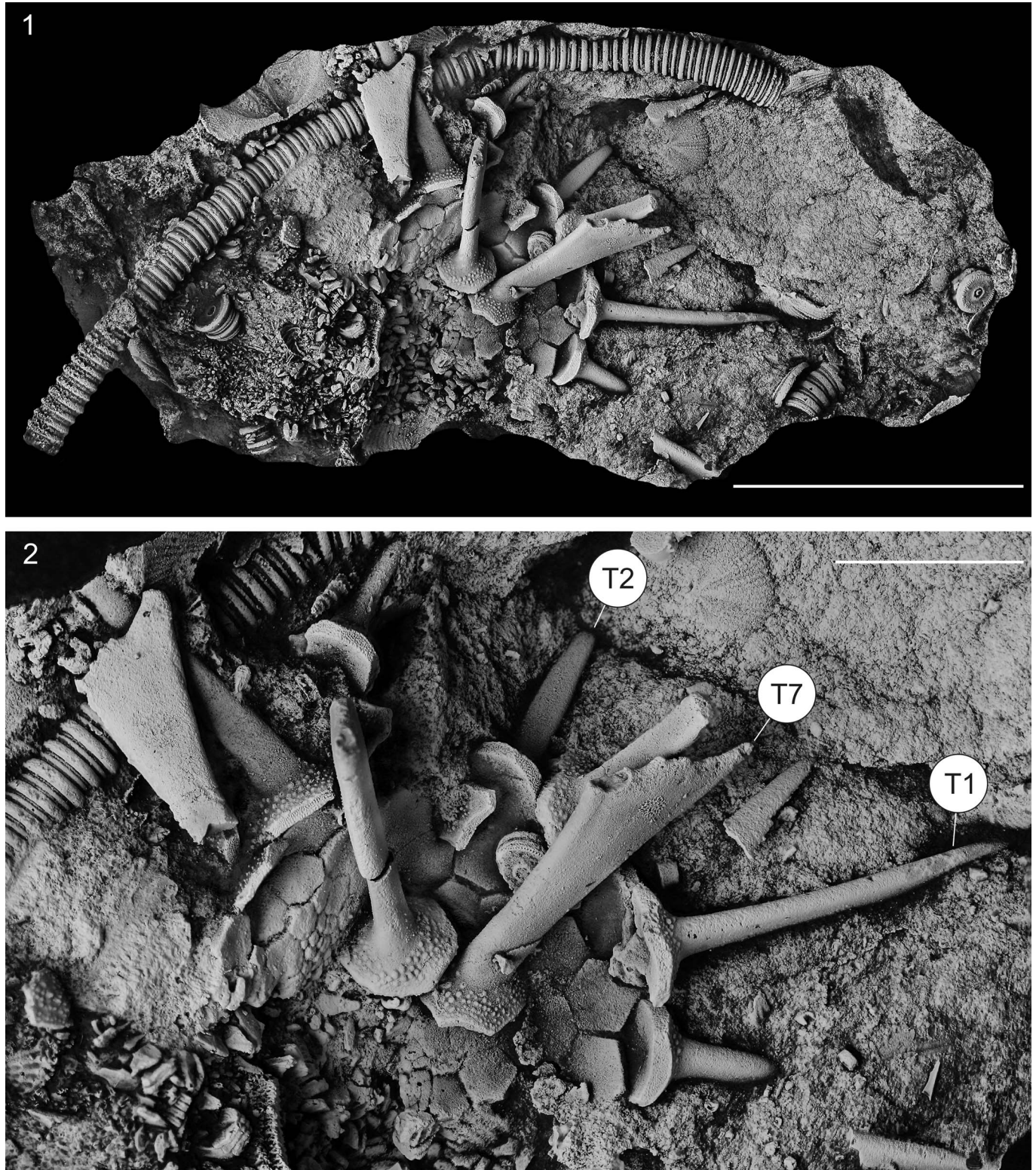


Figure 9. Recast holotype of *Monstrocrinus granosus* Schmidt, 1941 (no. SMF XXIII 113a) from the upper Emsian Mandeln Formation (*Polygnathus serotinus* Conodont Biozone) of Dietzhöhlzal–Mandeln in the Lahn–Dill district in central Hesse, north-northeast of Dillenburg. (1) Strongly disarticulated crown with longer part stem in matrix (until the present study, the stem was not interpreted as belonging to the individual); (2) detailed view, showing remains of spine types 1, 2, and 7 (T1, T2, T7) and granulated calyx plates. Scale bars = 3 cm in (1) and 1 cm in (2).

the result is a maximum total diameter of a calculated adult calyx of 20.0 cm. This value would probably be somewhat lower (~15 cm) if the spines were slightly inclined in the aboral

direction. The ratio of the maximum calyx diameter with preserved spines to maximum crown length (calyx with arms) is at least 1:1. On this basis, we calculated total crown height of

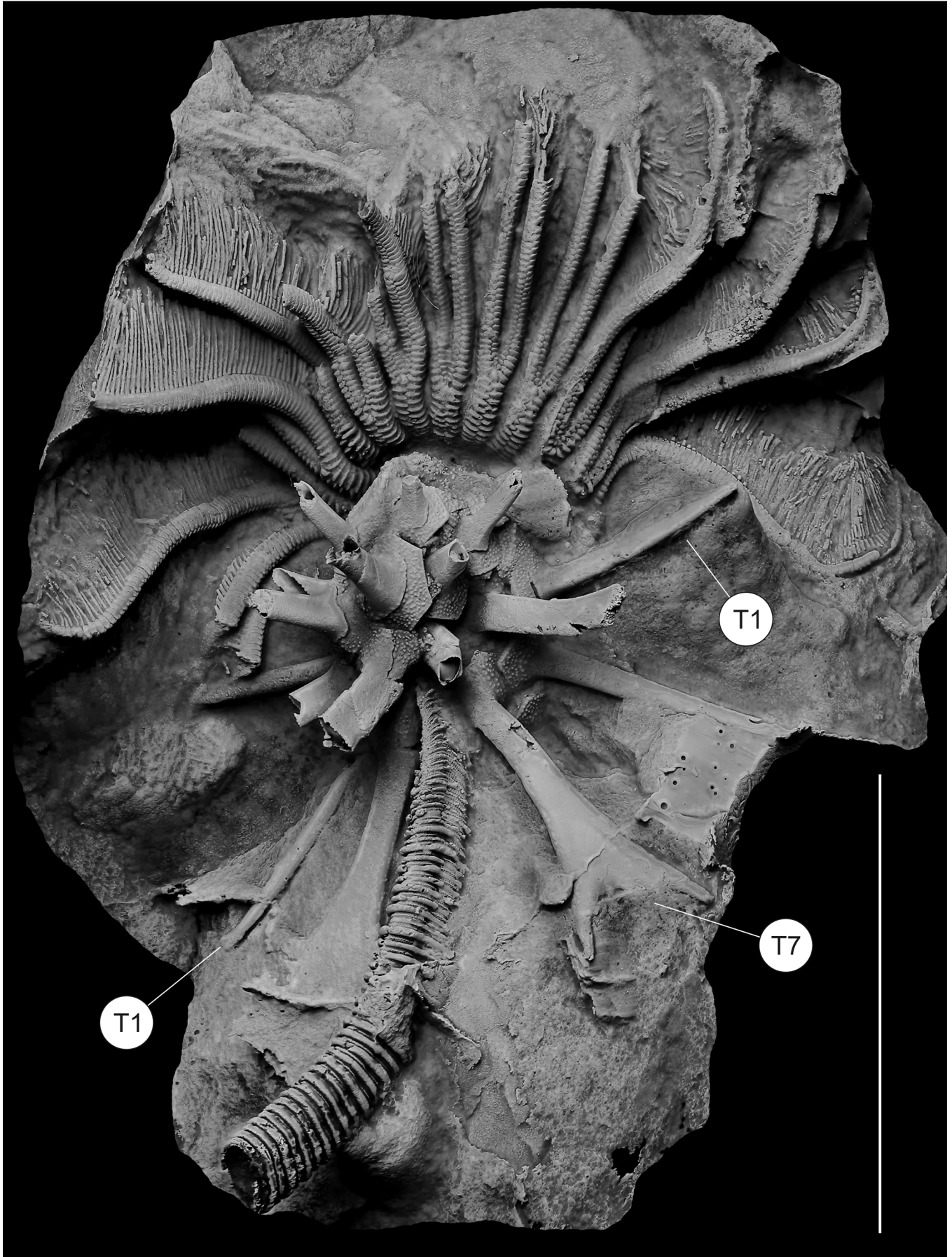




Figure 10. Lateral view of the cast of the most complete known *Monstrocrinus* (no. NHMMZ PWL 2021/6145-LS), *M. granosus* Schmidt, 1941, from the uppermost section of the Emsian *Orthocrinus* Beds (*Polygnathus costatus patulus* Conodont Biozone) of the former brick factory in the Osterbachtal, northwest of Olpe-Lütringhausen (administrative district Arnsberg, Sauerland, North Rhine–Westphalia, Germany). The specimen in matrix shows a longer part of stem, partly articulated spines, especially spine types 1 and 7 (T1 and T7), which are well preserved, and brachials preserved. The specimen shows evidence of non-lethal predation of its arms in which the distal portions are narrower than the proximal arms. Similarly, in two rays on the right portion of the organism, the free arm bifurcation is lower than in other arms, and the arms above the bifurcation are narrower. Scale bar = 3 cm.

40.0 cm (or 30.0 cm with slightly aborally inclined spines), as well as a truly “monstrous” fan when the arms were deployed in a feeding position.

Monstrocrinus securifer is distinguished from other species because it has a relatively large calyx, smooth calyx plate sculpturing, and shallow depressions at calyx plate triple junctions. It also had spine categories A (spines that are physically part of a calyx plate) and B (spine articulated with calyx plate), and the following spine types: (1) tapering point, (3) narrow paddle shaped, (4) broad paddled shape, (6) bifurcating, (7) forked, and (8) strongly asymmetrical with spines on outer margin. In contrast, *M. granosus* has a relatively small calyx, fine granulate calyx plate sculpturing, and shallow depressions at calyx plate triple junctions are absent. It also had spine categories A (spines that are physically part of a calyx plate) and B (spines articulated with calyx plate), and the following spine types: (1) tapering point, (2) blunt spine, (6) bifurcating, and (7) forked. The morphology of the calyx in *M. incognitus* is poorly preserved, but diagnostic characters that are known include smooth calyx plate sculpturing, spine categories A (spine that is physically part of a calyx plate) and B (spines articulated with calyx plate), and spine types (1) tapering point, (4) broad paddle-shaped spine, and (5) flat high spine.

Monstrocrinus granosus Schmidt, 1941
 Figures 3.2, 9–12

1941 *Monstrocrinus granosus* Schmidt, p. 217–218, text-figs. 61a, 61b1, 61b2, 61c, 61d, 61e1, 61e2.

1990 *Monstrocrinus granosus*; Le Menn, p. 151, 153–154, 156 (non fig. 3b).

Holotype.—Mold of a disarticulated crown with longer stem part in matrix, no. SMF XXIII 113a (recast and re-illustrated in Fig. 9), original of Schmidt (1941, p. 217, text-figs. 61a, 61.b1, 61.b2, 61.c, 61.d, 61.e1, 61.e2).

Emended diagnosis.—*Monstrocrinus* with a relatively small calyx; fine granulate calyx plate sculpturing; shallow depressions at calyx plate triple junctions absent; spine categories (A) spine that is physically part of a calyx plate and (B) spine articulated with calyx plate; and spine types (1) tapering point, (2) blunt spine, (6) bifurcating, and (7) forked.

Occurrence.—The species occurs in the upper Emsian Mandeln Formation (*Polygnathus serotinus* Conodont Biozone) within the “iron-shed greywacke schist” in the “Old Municipality Quarry” at the northern Hauberg Hill in Dietzhölztal–Mandeln in the Lahn–Dill district in central Hesse (Germany), north northeast of Dillenburg (type locality at UTM: 50°51′22.52″N, 8°20′51.41″E). The examined material is from the locus typicus of the type species *M. securifer*, the former brickworks mine

(slopes north, east, and south of the former brick factory, at UTM: 51°02′22.73″N, 7°51′51.02″E) in the Osterbachtal on today’s federal road B54, northwest of Olpe-Lütringhausen (administrative district Arnsberg, Sauerland, North Rhine–Westphalia, Germany). The classic site is located at the southeastern flank of the Middle Devonian Attendorn–Elsepe Double Syncline in the transition to the Lower Devonian Siegen Anticline and stratigraphically belongs to the uppermost section of the Emsian (Lower Devonian) *Orthocrinus* Beds (*Polygnathus costatus patulus* Conodont Biozone).

Emended description.—Calyx small in size, medium globe-shaped calyx with a shallow basal concavity, calyx height: width ratio 1.25; depressions at calyx plate triple junctions absent; finely granulate calyx plate sculpturing on plates and may be on adaxial portion of spines. Infrabasal plates confined to basal concavity, not visible in lateral view; presumably five infrabasal plates, pentagonal. Five basal plates form part of calyx base and proximal portion of the calyx vertical wall. Radial circlet with ten plates (all radial plates alternate with interradian plates); radial plates large, presumably five, hexagonal, approximately as high as wide, lacking broad folds. Calyx plates with long spines on at least basal plates, radial plates, proximal interradian plates, and some fixed brachials; spine categories (A) spine that is physically part of a calyx plate and (B) spine articulated with calyx plate; spine types (1) tapering point, (2) blunt spine, (6) bifurcating, and (7) forked. Proximal regular interradian plates large, hexagonal (more distal regular interradian plates not known). First interradian plate in regular interrays approximately the same size as radial plates and as high as wide. CD interray not known. Fixed brachials present but the number is unknown, median ray ridges absent. Tegmen unknown. Free arms presumably 20; high; one isotomous division; initially project obliquely downward, then abaxially, and finally obliquely upward. Proximal free brachials subrectangular, free brachials after division sharply convex, all brachials chisel biserial. Pinnules very long and slender, proximal pinnulars rectangular, higher than wide. Column circular, pentalobate lumen; nodal–internodal pattern N1; nodals wider than internodals. Proportions of different features on columnal facets: 12% narrow crenularium, 52% aereola, 8% perilumen, 28% lumen.

Remarks.—After recasting the holotype of *Monstrocrinus granosus* Schmidt, 1941 (no. SMF XXIII 113a), which was kindly provided by the Senckenberg Research Institute and Natural History Museum Frankfurt on the Main (Germany), important morphological characters came to light that were not recorded in the original description (compare Schmidt, 1941, p. 217, figs. 61a–e with our Fig. 9). The holotype of *M. granosus* is far more complete than previously reported. It is a highly disarticulated crown embedded together with an associated long part of the stem (Fig. 9). In addition, further

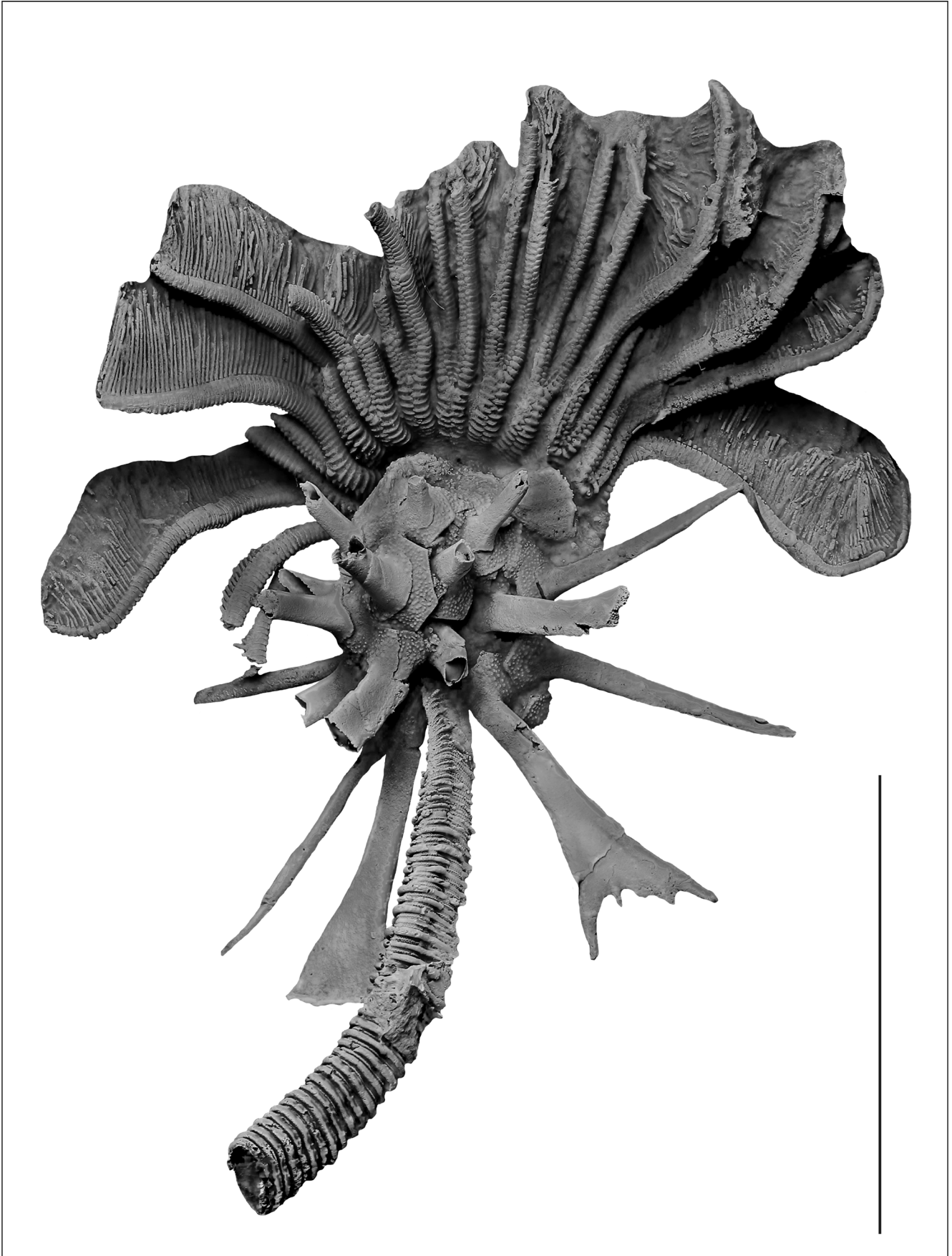


Figure 11. Digitally cropped view of the specimen shown in [Figure 10](#). Scale bar = 3 cm.

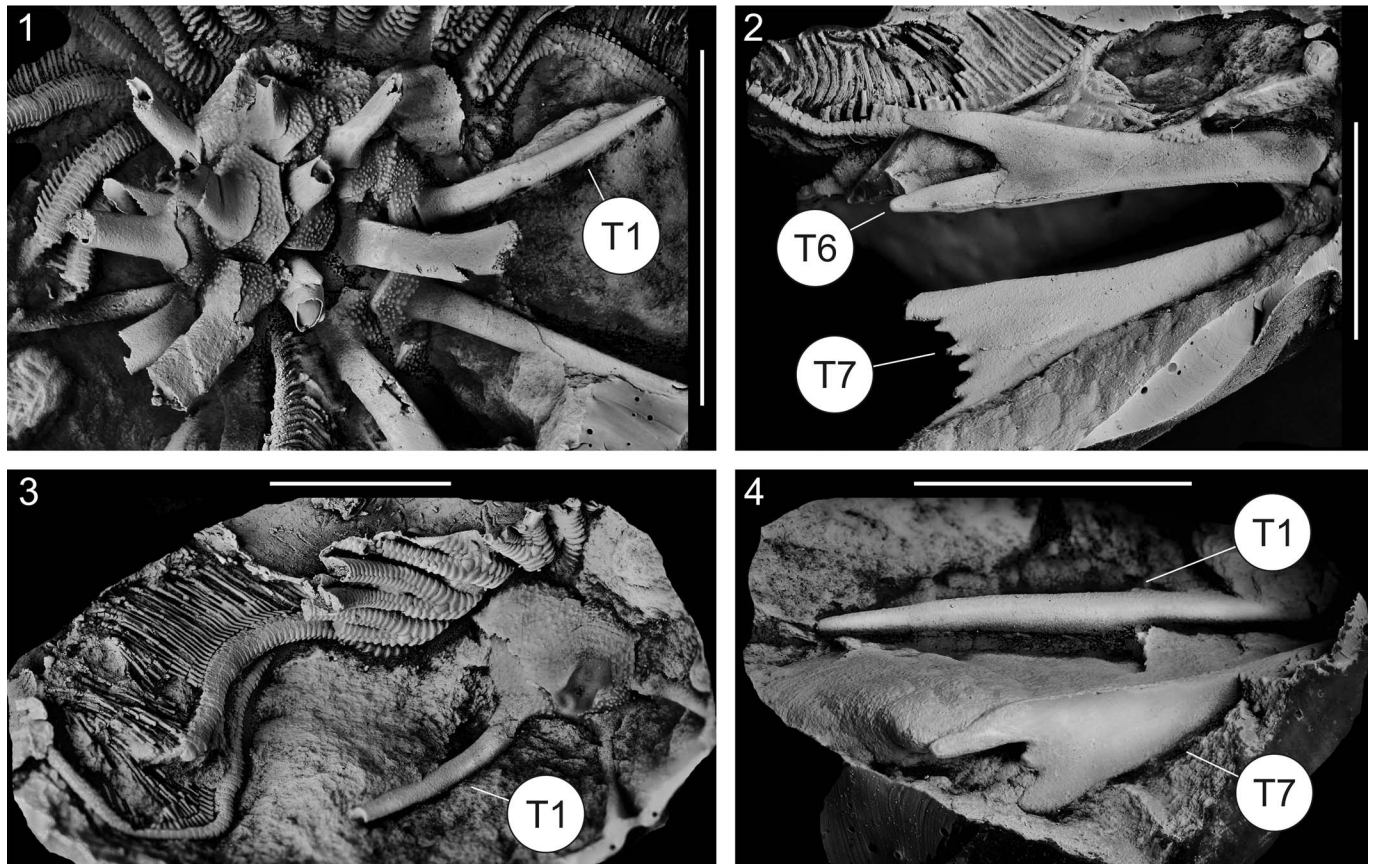


Figure 12. (1–4) Detail views of the specimen from Figures 10 and 11. (1) Lateral view of the spined calyx with well-preserved spine type 1 (T1). (2–4) Casts of the counter plates: (2) lateral view of two well-preserved spines of types 6 and 7 (T6, T7); (3) lateral view of part of the arms and calyx, showing spine type 1 (T1); (4) lateral view of spine types 1 and 7 (T1, T7). Scale bars = 2 cm in (1) and 1 cm in (2–4).

details of the spine morphology could be recorded. The previously unappreciated knowledge about the spine morphology led to an incorrect interpretation of a *granosus* spine by Le Menn (1990, p. 156, Fig. 3b). The latter author understood the prong-shaped extension of Schmidt's fig. 61b2 (1941, p. 217) as pointing proximally toward the calyx plate. In fact, it is not a backward-pointing prong, but a distally tapering bifurcation (see Schmidt, 1941, p. 217).

Whereas the holotype of *M. granosus* was found within the upper Emsian Mandeln Formation of the “Old Municipality Quarry” (Paleontological Ground Monument of the Federal State of Hesse, no. “Mandeln 991”) at the northern Hauberg Hill in Dietzhöhlztal–Mandeln in the Lahn–Dill district in central Hesse (Germany), the material examined by us comes from the uppermost section of the Emsian (Lower Devonian) *Orthocrinus* Beds of the *M. securifer* type locality, the former brickworks mine northwest of Olpe–Lütringhausen (administrative district Arnsberg, Sauerland, North Rhine–Westphalia, Germany). To date, this locality in Germany is the only fossil site where both species co-occur.

It should be noted that the endoskeletons of *M. granosus* are consistently smaller in size than in the comparatively larger type species *M. securifer*. *Monstrocrinus granosus* is compared to other species of *Monstrocrinus* in the remarks section of *M. securifer*.

Noteworthy is that the distal portion of some distal arms are of variable widths. Also, the position of the free arm division is

variable. One hypothesis is that these differences among free arms were a consequence of non-lethal predation on this specimen.

Monstrocrinus incognitus Scheffler et al., 2011
Figure 3.5, 3.6(?)

2011 *Monstrocrinus incognitus* Scheffler et al., p. 1189–1192, fig. 5.1–5.6.

Types.—The type material of *M. incognitus* is housed in the paleontological collection of the Departamento de Geologia e Paleontologia do Museu Nacional, Universidade Federal do Rio de Janeiro (UFRJ), Brazil, under institutional abbreviation no. MN8277-Id. (holotype) and nos. MN8277-Ia, and MN8277-Ib (paratypes).

Emended diagnosis.—*Monstrocrinus* with calyx size unknown; smooth calyx plate sculpturing; calyx plate triple junctions character unknown; spine categories (A) spine that is physically part of a calyx plate and (B) spine articulated with calyx plate; and spine types (1) tapering point, (4), broad paddle-shaped, (5), flat, high fan.

Occurrence.—*Monstrocrinus incognitus* was reported from the western edge of the Parnaíba Basin from three outcrops

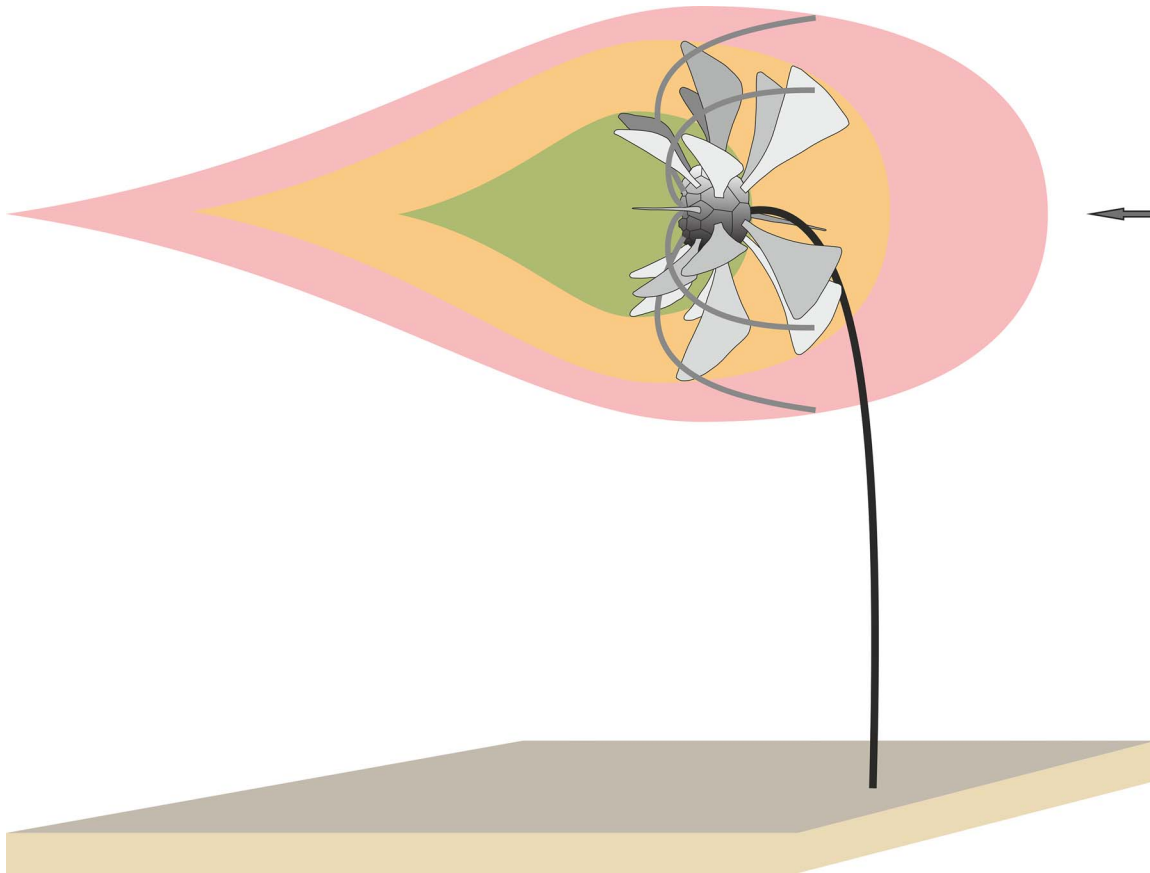


Figure 13. Schematic reconstruction of *Monstrocrinus* in feeding posture (based on the model of *Pterotocrinus depressus* by Baumiller and Plotnick, 1989, p. 323, fig. 10); note arms are not in this reconstruction. The arrow indicates the current direction. In this model, the spines of *Monstrocrinus* serve as stabilizing fins or rudders, allowing the passive maintenance of an efficient feeding posture in moving water. While the crown is lifted into the water column by the stem and the arms were stretched out in the filtration fan feeding position, an aboral-to-oral water flow through the spines create a zone of slower recirculating water downstream toward the arms and the oral side of the calyx. The zone shown in pink, yellow, and green indicate fast, medium, and slower recirculating water downstream.

(Fazenda Encantada II, Estância Cantilena, and Mirante Taquaruçu) in the district of Taquaruçu (Municipality de Palmas, state of Tocantins, Brazil), and, according to Scheffler et al. (2011), occurs in outcrops positioned near the base of the middle to upper Eifelian Pimenteira Formation.

Remarks.—*Monstrocrinus incognitus* is characterized in particular by the distinctive type 4a spines, which have a shorter length and a generally shorter and taller neck compared to those in *M. granosus* and *M. securifer*. This feature clearly justifies designation of a distinct species.

Scheffler et al. (2006, p. 238, fig. 3A–3E) described “*Monstrocrinus securifer*” from the middle Eifelian Maecuru Formation along the Maecuru River in the northwestern part of the State of Pará in Brazil. In our opinion, this material belongs either to *M. incognitus* or to another species of *Monstrocrinus* (compare Fig. 3.5 and 3.6 of the present study). Therefore, it could be possible that the species diversity of *Monstrocrinus* in Brazil is higher than currently known (further investigations are necessary).

Results and discussion

Schmidt (1941) described the base of the *Monstrocrinus* calyx from a specimen that is primarily an internal mold of articulated

infrabasal and basal plate circlets (a mold of this specimen is illustrated in Fig. 7). The original interpretation of *Monstrocrinus* was that this crinoid lacked a column as an adult; however, the calyx–proximal columnal attachment would be visible on the opposite surface of the infrabasal circlet. The most complete, new specimen has a long segment of column projecting outward from the basal concavity, which confirms that the *Monstrocrinus* crown was attached to a column as an adult. Thus, a free-living life mode of a passively rolling or drifting crinoid (Schmidt, 1941; Etensohn, 1984; Le Menn, 1990; Hauser, 2012) is refuted. Instead, the life mode *Monstrocrinus* should be interpreted as an attached, stalked echinoderm. Therefore, the previous interpretations of the calyx spines as floating spines, crawling spines, or skeletal elements resting on the sea floor must be reinterpreted, because the spines were most likely lifted above the bottom substrate, as was the entire crown.

Three functional hypotheses for the long spines are: 1, antipredatory; 2, modification of currents to enhance feeding; and 3, stability of the crown in a current. We regard the antipredatory interpretation for the spines to be the most probable, which would be consistent with increasing predation pressure during the Mid Paleozoic Marine Revolution (Meyer and Ausich, 1983; Signor and Brett, 1984; Brett and Walker, 2002; Baumiller and Gahn, 2004, 2012; Gahn and Baumiller, 2005, 2010).

Further evidence of non-lethal predation on *Monstrocrinus* is the occurrence of arms in which the distal portion of the arms are narrower than the proximal arms. This condition occurs in several arms (Fig. 10) and is consistent with non-lethal predation. Similarly, in two rays on the right portion of the organism, the free arm bifurcation is lower than in other arms and the arms above the bifurcations are narrower. This is also consistent with regeneration following non-lethal predation (see Meyer and Ausich, 1983; Signor and Brett, 1984; Brett and Walker, 2002; Baumiller and Gahn, 2004, 2012; Gahn and Baumiller, 2005, 2010).

Spines producing eddying that may have enhanced feeding is a second hypothesis for the spines. In this case, perhaps eddying of aboral–oral flow of water through the spines slowed water that passed into the arms and directed a larger sample of water than only straight-line currents (Fig. 13).

It is also possible that the spines provided rotational stability for the crown, similar to that recognized by Baumiller and Plotnick (1989) in a study on the function of wing plates of the Mississippian camerate crinoid *Pterotocrinus depressus* Lyon and Casseday, 1860. However, the fact that spine placement, size, and shape varied around the calyx may not support this third hypothesis as an adaptive strategy.

Acknowledgments

We are especially grateful to R. Bersch (Dortmund) who discovered specimen NHMMZ PWL 2021/6145-LS from Olpe about 40 years ago and donated it to one of us (MJP). E. Schindler and M. Ricker (Senckenberg Research Institute and Natural History Museum Frankfurt on the Main, Germany) kindly provided the holotype of *Monstrocrinus granosus* for reexamination. The same thanks go to G. Heumann (Goldfuß-Museum, Institute for Geosciences, Rhenish Friedrich Wilhelm University of Bonn, Germany), who made the type material of *M. securifer* available to us. We thank S.M. Scheffler (Federal University of Rio de Janeiro, UFRJ, Brazil) for his willingness to discuss and for important stratigraphic and taxonomic information on the Brazilian *Monstrocrinus*. We are curious to learn further insights and details of Brazilian occurrences. We thank U. Hein (Solingen), and H.-P. Hein (Wermelskirchen) for discovery and donation of several studied crinoids, as well as for numerous important comments. We thank S. Zamora (editor, Journal of Paleontology) and P. Gorzelak (associate editor, Journal of Paleontology), and F. J. Gahn, and one anonymous reviewer for their reviews that greatly enhanced this manuscript.

Declaration of competing interest

There is no conflict of interest with any author.

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